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Proposal of *Marbefia*, gen. n. and *Inermiphonte*, gen. n., including updated keys to the species of *Pseudonychocamptus* Lang, 1944 and *Paralaophonte* Lang, 1948 (Copepoda, Harpacticoida, Laophontidae)

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Abstract

Both sexes of the enigmatic laophontid species *Pseudonychocamptus carthyi* Hamond, 1968 (Copepoda, Harpacticoida) are redescribed in detail based on type and other material from Norfolk, England. The species exhibits marked differences with other *Pseudonychocamptus* species and is consequently fixed as the type of a new genus *Marbefia*, **gen. n.**, being defined by the following autapomorphies: (1) P2–P4 enp-2 (except P4 enp-2 in ♂) inflated, with two parallel rows of flimsy setular extensions; (2) P4 with sexually dimorphic setation on enp-2 (outer distal seta reduced in ♀, very long in ♂); and (3) antennule ♀ with spinules along posterior margins of segments 1–6. *Laophonte danversae* Hamond, 1969, "Laophontid male, ?gen., ?sp." *sensu* Hamond (1969) [renamed as *Inermiphonte hamondi,* **sp. n.**] and *Laophonte ?drachi* Médioni & Soyer, 1966 are collectively placed in a new genus *Inermiphonte*, **gen. n.** which shares as sistergroup relationship with *Harrietella* T. Scott, 1906. *Marbefia*, **gen. n.** is considered sister to a clade comprising the genera *Pseudonychocamptus* Lang, 1944, *Pilifera* Noodt, 1952, *Inermiphonte*, **gen. n.** and *Harrietella*. *Pseudonychocamptus kolarovi* Apostolov, 2008 is transferred to *Paralaophonte* whereas Chislenko's (1967) record of *P. koreni* Sars, 1908a is considered doubtful. Willey's (1935) variety "*fissirostris*" of *Paralaophonte brevirostris* (Claus, 1863) is rejected pending a thorough analysis of the variability in the *P. brevirostris* complex of species. *P. congenera mediterranea* Lang, 1948 appears to be more closely related to *P. lacerdai* Jakobi, 1953 than to its nominotypical subspecies *P. congenera congenera* (Sars, 1908b) whereas

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P. pacifica galapagoensis Mielke, 1981 (here upgraded to full specific rank) is more similar to *P. brevirostris* than to its nominotypical subspecies *P. pacifica pacifica* Lang, 1965. A new species, *Paralaophonte pallaresae*, **sp. n.** is proposed for *P. gracilipes* Brady, 1910 *sensu* Pallares (1968). The potentially paraphyletic status of the genus *Paralaophonte* is discussed. Dichotomous identification keys are provided for the valid species of *Pseudonychocamptus* Lang, 1944 and *Paralaophonte* Lang, 1948.

Keywords

Copepoda, Laophontidae, *Inermiphonte*, gen. n., *Loureirophonte*, *Marbefia*, gen. n., *Paralaophonte*, *Pseudonychocamptus*, *Paralaophonte kolarovi,* comb. n., *P. pallaresae*, sp. n., *Inermiphonte hamondi*, sp. n., identification keys

Introduction

In one of his papers dealing with the Laophontidae from Norfolk, Hamond (1968) described a new species in the genus *Pseudonychocamptus* Lang, 1944 for a single female found in washings of intertidal colonies of the hydroid *Hartlaubella gelatinosa* (Pallas, 1766) (as *Laomedea gelatinosa*) collected under the Hunstanton pier. *Pseudonychocamptus carthyi* Hamond, 1968 has been recorded in the literature only once since its original description and the male has remained unknown. The only other record is that by Holmes and Minchin (2000) who collected a single female from a *Serpula vermicularis* L. reef at 4 m depth near the ferry pier on the south side of Killary Harbour, Co. Galway, Ireland.

In their review of the genus *Paronychocamptus* Lang, 1948, Lee and Huys (1999) identified a lineage within the subfamily Laophontinae, consisting of the genera *Pseudonychocamptus*, *Pilifera* Noodt, 1952, *Weddellaophonte* Willen, 1996 and *Heteronychocamptus* Lee & Huys, 1999. This "*PWPH*-clade" is primarily characterized by a distinctive type of swimming leg sexual dimorphism. In all four genera, females possess a seta on the proximal endopod segment of P3 and P4 but males consistently lack this armature element (Table 1). Lee and Huys (1999) also recognized a close relationship between *Pilifera* and *Pseudonychocamptus* but remarked that *P. carthyi*, by virtue of its primitive swimming leg armature, probably occupies a position close to the ancestor of the *PWPH*-clade. Pending the discovery of the unknown male, they refrained from attributing the species to a new genus. In this paper we have re-examined additional material of *P. carthyi* from Norfolk, which had been deposited in the collections of the Natural History Museum by Dr Richard Hamond. These specimens, representing both sexes, form the basis for a redescription of the female and the first description of the male, providing morphological evidence for its assignment to a new genus *Marbefia*.

Material and methods

Before dissection, the habitus was drawn from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid and the dissected parts were mount-

Table 1. Comparison between *Harrietella* and laophontid genera/species displaying sexual dimorphism in setation of P3–P4 enp-1 (exp = exopod; enp = endopod; benp = baseoendopod; A1 = number of antennulary segments; P3 ♂ = number of endopodal segments); losses in males indicated in boldface; species here reassigned to *Inermiphonte* gen. n. marked by *.

		A1	P2		P3		P4		P5		P3 ♂
			exp	enp	exp	enp	exp	enp	exp	benp	
Weddellaophonte	♀	6	0.1.123	0.220	0.1.223	1.121	0.1.223	1.120	5	5	–
	♂	–	0.1.123	0.220	0.1.223	**0**.0.120	0.1.223	**0**.120	4	2	3
Heteronychocamptus	♀	7	0.1.123	[0–1].120	0.1.123	1.121	0.1.12[2–3]	1.121	4-5	5	–
	♂	–	0.1.123	[0–1].120	0.1.123	**0**.0.020	0.1.12[2–3]	**0**.121	4	2	3
Marbefia, gen. n.	♀	7	0.1.123	0.220	0.1.223	1.321	0.1.223	1.121	6	5	–
	♂	–	0.1.123	0.220	0.1.223	**0**.220	0.1.223	**0**.121	4	2	2
Pilifera	♀	7	0.1.123	0.120	0.1.123	1.221	0.1.122	1.121	5	5	–
	♂	–	0.1.123	0.120	0.1.123	**0**.020	0.0.022	**0**.020	4	2	2
Pseudonychocamptus	♀	7	0.1.123	0.220	0.1.123	1.[1–2]21	0.1.123	1.121	5-6	5	–
	♂	–	0.1.123	0.[01]20	0.1.123	**0**.[0–2]20	0.1.123	020	3-4	2	2
**Laophonte danversae* [a]	♀	7	0.1.023	0.120	0.1.023	0.121	0.0.022	1.021	6	5	–
	♂	–	0.1.023	0.120	0.1.023	0.020	0.0.022	**0**.021	5	2	2
*Laophontid male, ?gen., ?sp. [b]	♂	–	0.1.023	0.220	0.1.023	0.120	0.0.023	0.021	4	2	2
**Laophonte drachi* [c]	♀	6	0.0.023	0.120	0.0.023	0.021	0.0.022	0.021	6	4	–
	♂	–	0.0.023	0.120	0.0.023	0.020	0.0.022	0.021	4	2	2
Harrietella	♀	6	0.1.023	0.020	1.0.023	0.121	0.02[3–4]	020	4–5	3-4	–
	♂	–	0.1.023	0.020	1.0.023	0.121	0.02[3–4]	020	4	1	2

[a] Hamond (1969) noted variability in the armature of P4 endopod ♀ (1.021 or 0.020 or 1.020); examination of additional material showed 1.021 to be the normal condition (as figured by Hamond 1969: his Fig 14).

[b] *sensu* Hamond (1969: 9) = *Inermiphonte hamondi*, sp. n.

[c] Note that Médioni and Soyer's (1966: 1057) armature formula is given in corrected format here to account for the small inner distal seta on P2–P4 exp-3 (figured by the authors for P3 but omitted in their formula; overlooked in P4; P2 was not figured). Wells (2007: 436, 458) had already amended the setal counts for P2–P3.

ed in lactophenol mounting medium. Broken glass fibres were added to prevent the animal and appendages from being compressed by the coverslip and to facilitate rotation and manipulation, allowing observation from all angles. Preparations were subsequently sealed with Glyceel or transparent nail varnish. All drawings were prepared using a camera lucida on a Zeiss Axioskop differential interference contrast microscope. Total body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. Measurements were made with an ocular micrometer. Scale bars in illustrations are in µm. The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: ae, aesthetasc; P1–P6, for swimming legs 1–6; exp, enp and benp for exopod, endopod and baseoendopod, respectively; exp (enp)-1 (-2, -3) to denote the proximal (middle, distal) segments of a ramus; NHM, Natural History Museum (London). The term 'acrothek' denotes the trifid setal structure found primitively on the apical margin of the distal antennulary segment (Huys and Iliffe 1998).

Results

Order Harpacticoida Sars, 1903
Family Laophontidae T. Scott, 1905

***Marbefia*, gen. n.**
urn:lsid:zoobank.org:act:5B070367-A759-44B2-931C-7D9A49AC6AC4

Diagnosis. Laophontidae. Body linear, not dorsoventrally depressed. Integument of cephalothorax and body somites covered with tiny spinules; posterior margins of somites smooth, with spinule rows dorsally and ventrally. Rostrum delimited at base; broadly triangular, prominent. Genital double-somite ♀ with lateral incisions and ventrolateral internal chitinous ribs marking original segmentation. Pleural extensions of ♀ abdominal somites well developed. Caudal ramus cylindrical, subrectangular and as long as wide; inner margin with long spinules; with 7 setae; setae IV and V well developed, pinnate; seta VI reduced, setiform. Anal operculum spinulose.

Sexual dimorphism in antennule, P3–P4 endopods, P5, P6 and in genital segmentation.

Antennule slender and 7-segmented in ♀; 8-segmented and subchirocer with 3 segments distal to geniculation in ♂; segments with spinular ornamentation along anterior margin of segments 1–4 in ♀ and 1–3 in ♂; segments 1–2 without processes; with aesthetasc on segment 4 (♀) or 5 (♂); acrothek on apical segment consisting of 2 setae and one aesthetasc. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Mandibular palp elongate, 1-segmented; with one basal, one exopodal and 3 endopodal setae. Maxillule with defined exopod bearing 2 setae. Maxilla with 3 endites on syncoxa; endopod represented by 4 setae. Maxilliped elongate; syncoxa with 2 setae; basis without distinct ornamentation; endopodal claw long and curved, with one accessory seta.

P1 long, with elongate coxa and basis; with 3-segmented exopod, exp-2 1.6 times as long as exp-1, exp-3 with 2 short and 2 geniculate setae; endopod stout, enp-1 without inner seta, enp-2 with minute seta and long minutely denticulate claw. Swimming legs P2–P4 with 3-segmented exopods and 2-segmented endopods. P2–P4 enp-2 swollen, with double row of flimsy setular extensions along outer lateral margin (except for P4 in ♂); inner seta of P3–P4 enp-1 present in ♀ but absent in ♂. P3 enp-2 produced into straigth spiniform apophysis in ♂ (homologous with outer spine of enp-2 in ♀). Armature formula of swimming legs 2 to 4 (P2–P4) as follows:

	Exopod	**Endopod**
P2	0.1.123	0.220
P3	0.1.223	1.321 [0.220 in ♂]
P4	0.1.223	1.121 [0.121 in ♂]

P5 with separate exopod and baseoendopod. Exopod elongate with 6 setae in ♀ and 4 setae in ♂. Endopodal lobe well developed in ♀, subrectangular, with 5 setae. Baseoendopods fused medially in ♂; endopodal lobes rudimentary, with 2 setae each.

P6 forming well developed operculum with 2 small setae in ♀; asymmetrical in ♂ (with dextral or sinistral configuration), with outer distal corner produced into conical process bearing 2 well developed elements.

Type and only species. *Pseudonychocamptus carthyi* Hamond, 1968 = *Marbefia carthyi* (Hamond, 1968), comb. n.

Etymology. The name of the new genus honours the advances in our understanding of marine ecosystem functioning stimulated by the MarBEF Network of Excellence in Marine Biodiversity and Ecosystem Functioning. Gender: feminine.

Marbefia carthyi (Hamond, 1968), comb. n.

Figs 1–6

Pseudonychocamptus carthyi Hamond, 1968

Type locality. England, Norfolk, Hunstanton; in washings of colonies of *Hartlaubella* (as *Laomedea*) *gelatinosa* (Pallas, 1766) (Hydrozoa, Campanulariidae) attached to concrete lumps found in little shallow pools under the pier; for associated fauna see Hamond (1968: 176).

Material examined. (1) **Holotype.** ♀ dissected on one slide (reg. no. NHM 1967.10.2.2), from type locality, collected on 2 April 1957 by R. Hamond;

(2) one ♀ dissected on 12 slides, one ♂ dissected on 9 slides, one ♀ and one ♂ used for SEM examination, and two ♂♂ in 70% ethanol; all specimens collected from Station MB.17 (53°10.34′N, 00°56.34′E) on 6 May 1992 by R.

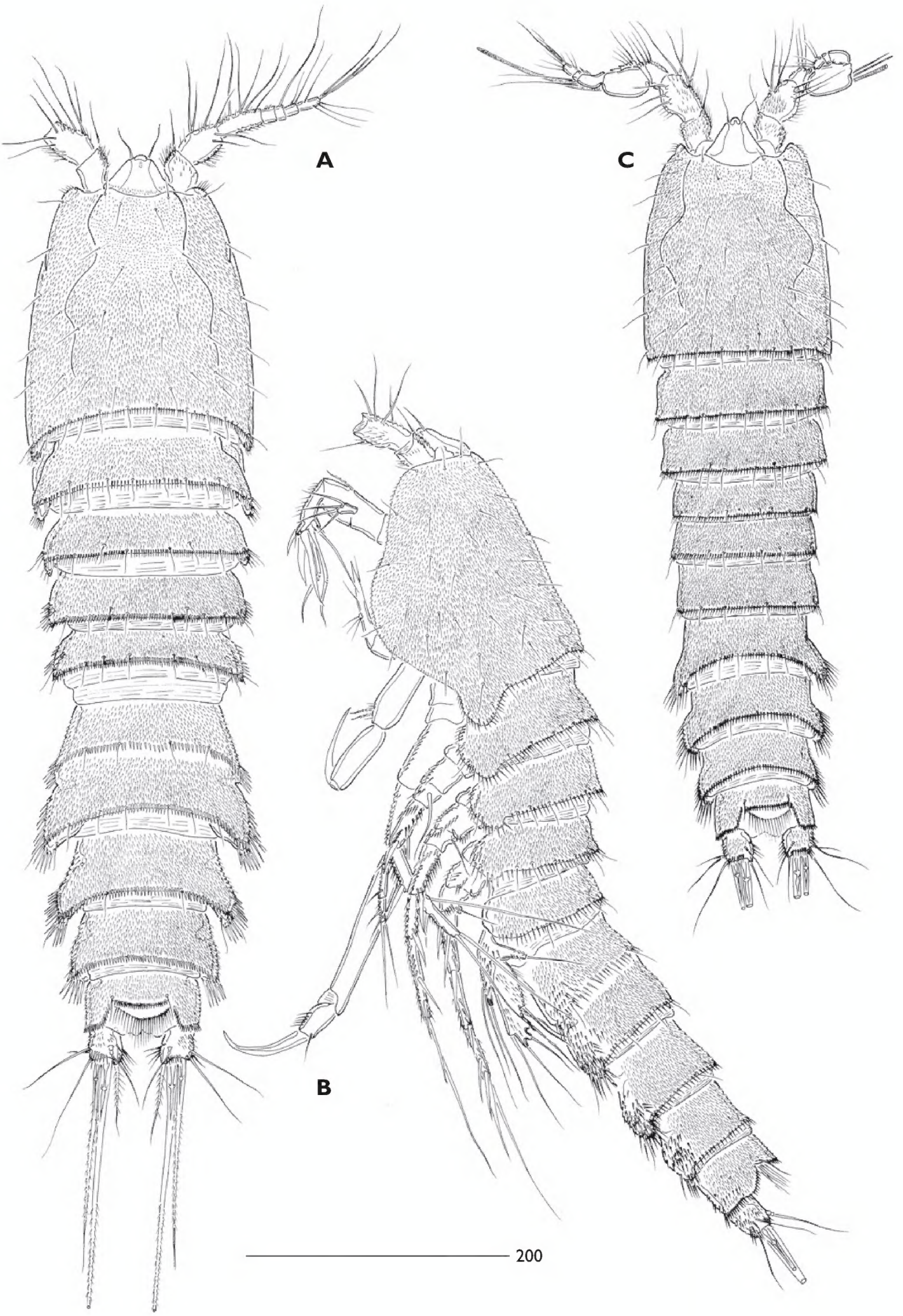

Figure 1. *Marbefia carthyi* (Hamond, 1968), comb. n.: **A** habitus ♀, dorsal **B** habitus ♀, lateral **C** habitus ♂, dorsal.

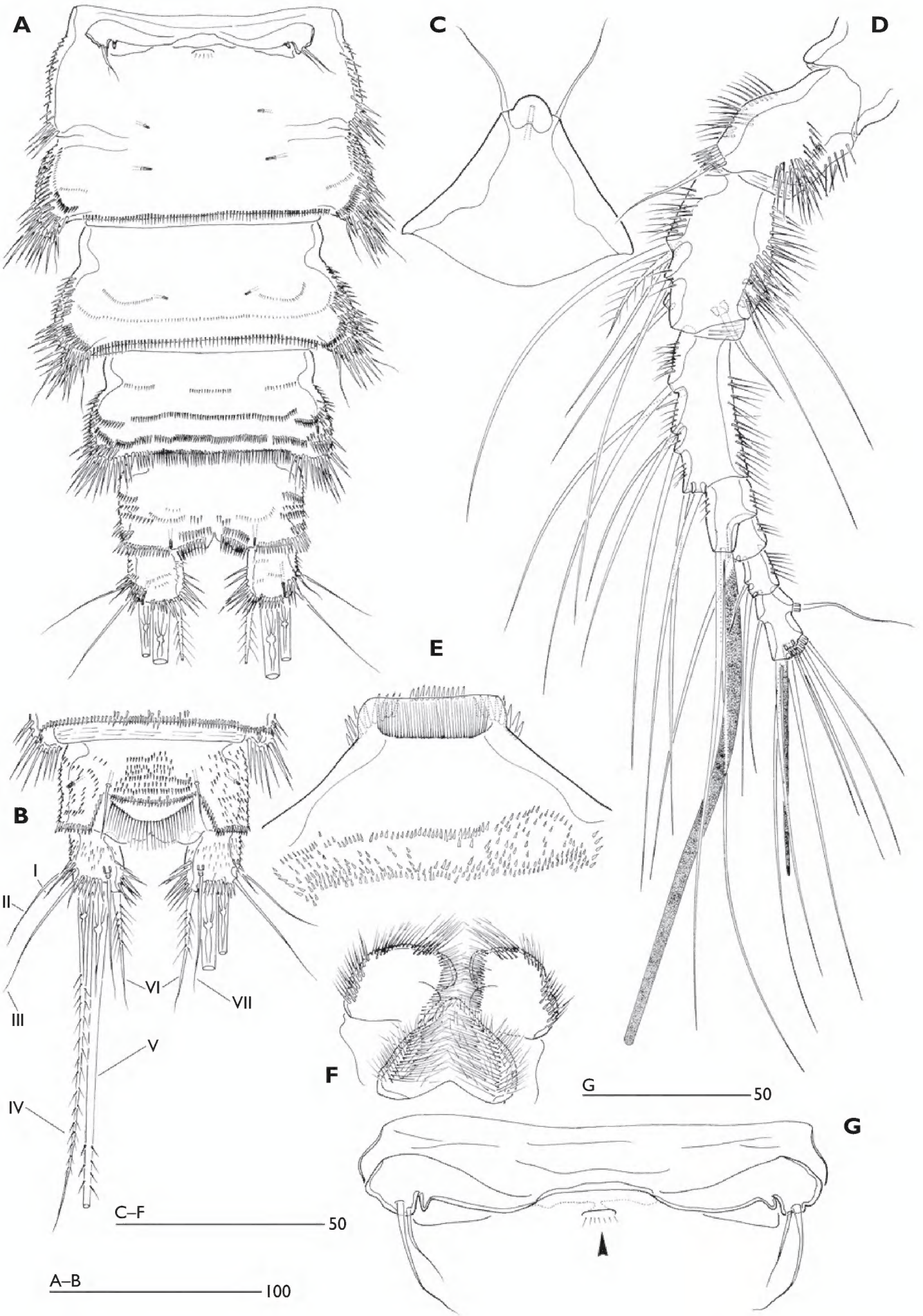

Figure 2. *Marbefia carthyi* (Hamond, 1968), comb. n. (♀): **A** urosome, ventral [excluding P5-bearing somite] **B** anal somite and caudal rami, dorsal **C** rostrum, dorsal **D** antennule, ventral **E** labrum, anterior **F** paragnaths, anterior **G** genital area with P6 [copulatory pore arrowed].

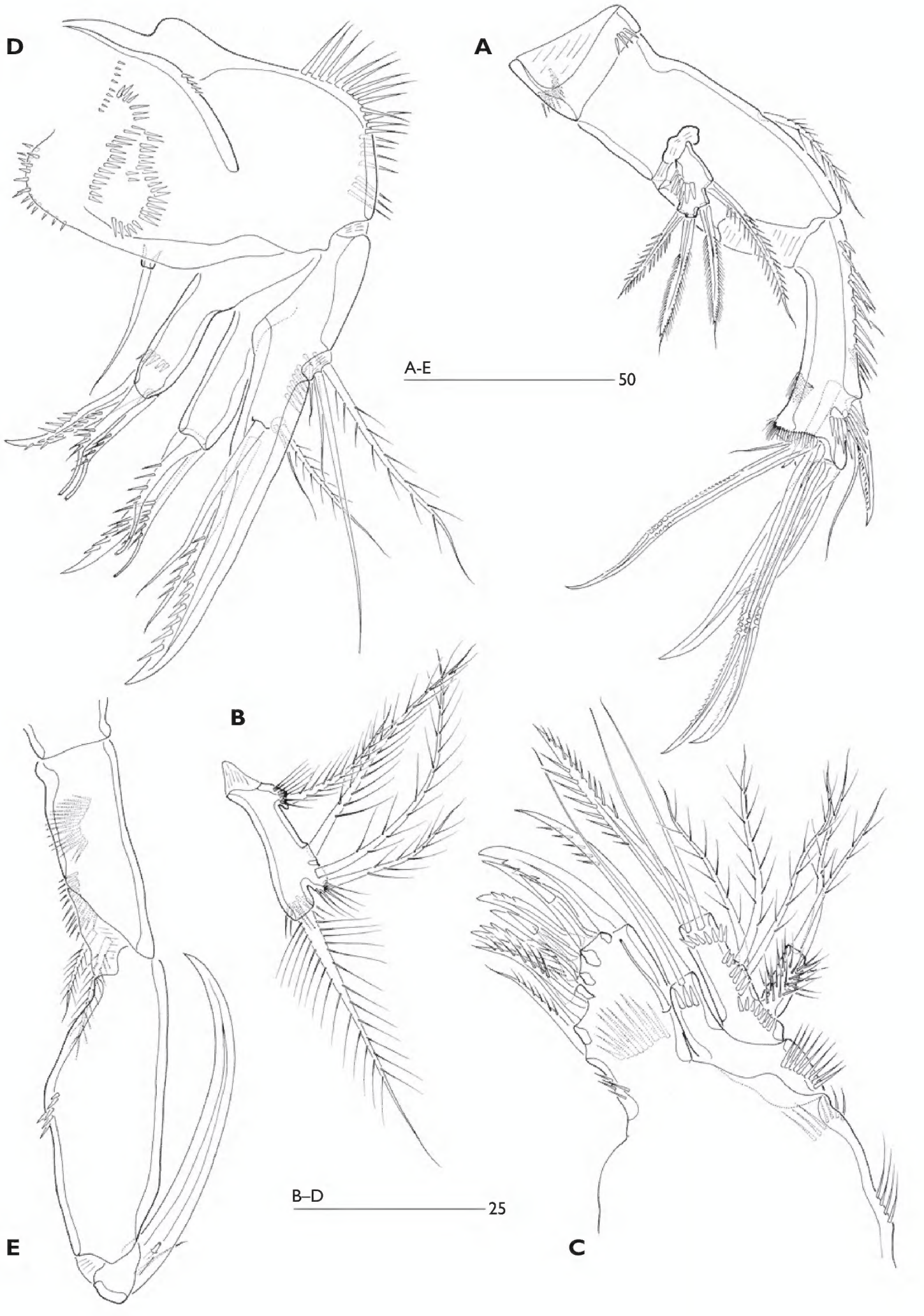

Figure 3. *Marbefia carthyi* (Hamond, 1968), comb. n. (♀): **A** antenna **B** mandibular palp **C** maxillule, anterior **D** maxilla, posterior **E** maxilliped, posterior.

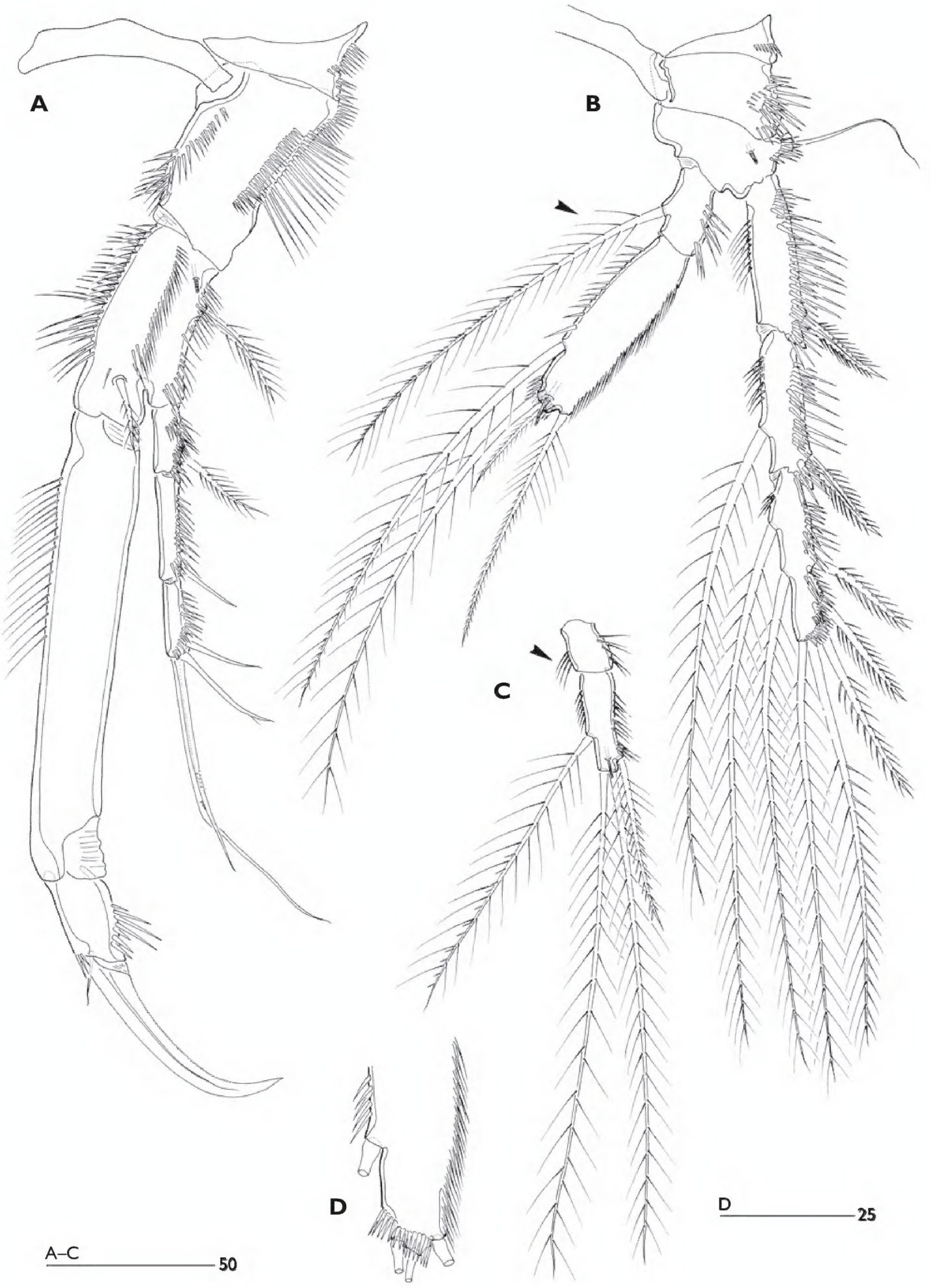

Figure 4. *Marbefia carthyi* (Hamond, 1968), comb. n.: **A** P1 ♀, anterior **B** P4 ♀, anterior [inner seta on enp-1 arrowed] **C** P4 endopod ♂, anterior [spinular rows on enp-1 arrowed] **D** distal part of P4 endopod ♀, posterior.

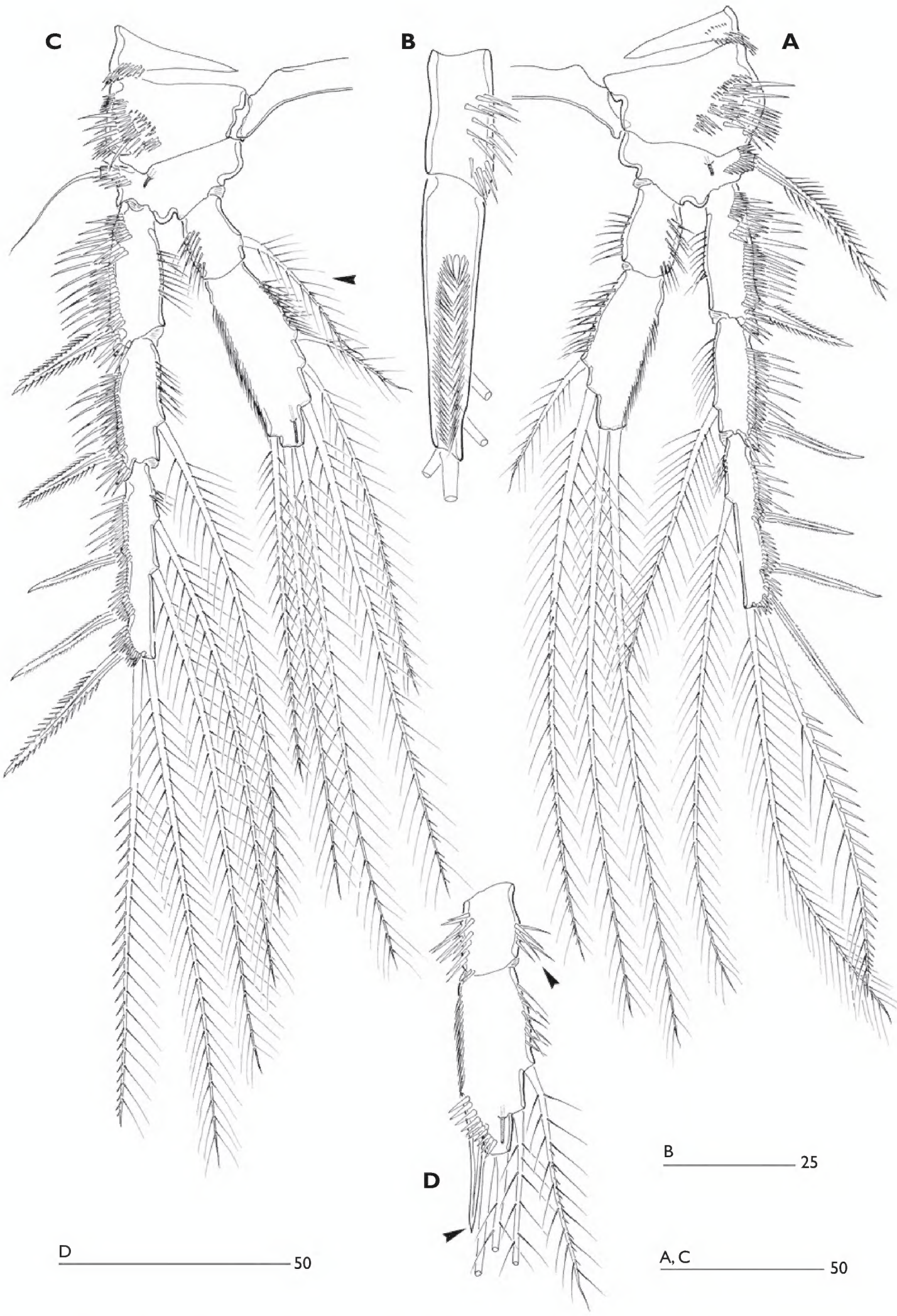

Figure 5. *Marbefia carthyi* (Hamond, 1968), comb. n.: **A** P2 ♀, anterior, **B** P2 endopod ♀, outer lateral **C** P3 ♀, anterior [inner seta on enp-1 arrowed] **D** P3 endopod ♂ [spinules on enp-1 and apophysis on enp-2 arrowed].

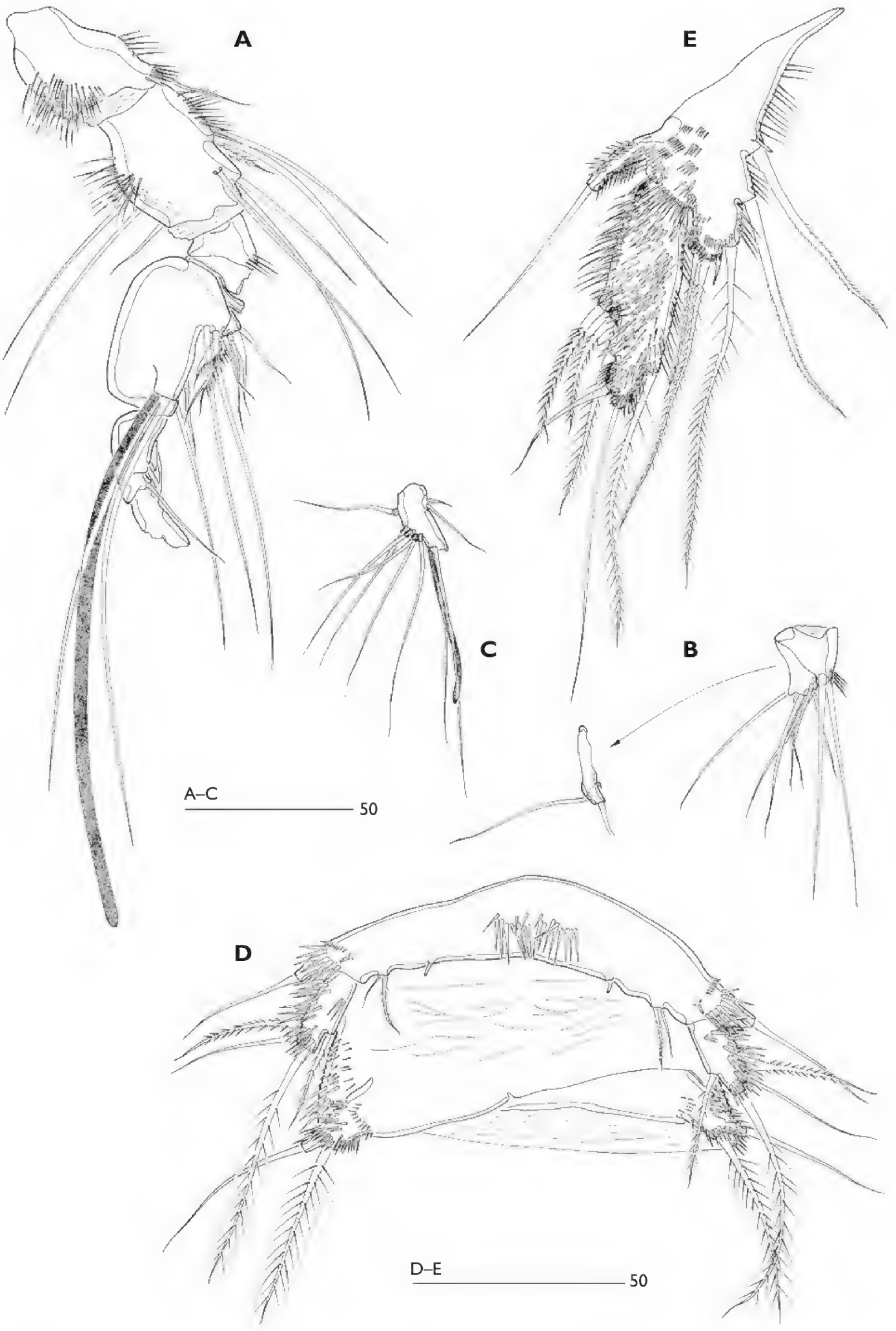

Figure 6. *Marbefia carthyi* (Hamond, 1968), comb. n.: **A** antennule ♂, ventral [armature on segments 3, 4 and 8 omitted] **B** antennulary segments 3 (right) and 4 (left) ♂ **C** antennulary segment 8 ♂ **D** P5 and P6 ♂, anterior **E** P5 ♀, anterior.

Hamond (reg. nos. NHM 1993.312–321); depth 12–13 m; fine sand with high silt content;

(3) one ♀ (reg. no. NHM 1998.588) re-identified by F. Fiers in 1998, found among *Pseudonychocamptus koreni* (Boeck, 1873) specimens (reg. no. NHM 1967.10.31–70) collected during the 1966 University of London Sub-Aqua Club expedition to the Isles of Scilly; Great Britain Rock, off St Mary's; algal debris at LWN, among bryozoans (*Cellaria*, *Lepralia*) and hydroids (*Sertularia*), 27 m; July 1966 (*cf.* Wells 1970: 267).

Description. Female. *Body* (Figure 1A, B). Total body length 696–738 µm (n=2; mean 717 µm). Largest width at posterior margin of cephalic shield (174 µm). Urosome gradually tapering posteriorly (Figure 1A). Rostrum triangular (Figure 2C), with pair of sensilla near apex; midventral tube-pore in subapical position; completely defined at base. Cephalothorax with posterior margin fringed with small spinules; pleural areas well developed and rounded with lobate posterolateral angles; entire surface covered with tiny spinules as illustrated in Figure 1A, B; sensilla and few pores present as illustrated in Figure 1A, B. Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; posterior margins fringed with small spinules. Body constricted between individual somites. Urosome (Figures 1A, B; 2A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. Abdominal half of genital double-somite and second abdominal somite with lateral lobate extensions. All urosomites with surface ornamentation consisting of small spinules dorsally and laterally; ventral surface largely naked except for few rows of spinules and paired tube-pores; ventral hind margin with large spinules laterally and small spinules medially (Figure 2A). Hyaline frills of urosomites not distinct. Genital double-somite (Figures 1A; 2A) with transverse, surface ridge dorsally and laterally, indicating original segmentation; completely fused ventrally. Genital field (Figure 2G) with medium-sized copulatory pore (arrowed in Figure 2G) located in median depression; gonopores fused medially forming single genital slit covered on either side by operculum derived from sixth leg; P6 with small protuberance bearing 2 bare setae; small triangular process located on medial side adjacent to protuberance. Anal somite (Figure 2B) with spinular ornamentation and pair of dorsal tube-pores; anal operculum well developed, bearing row of minute spinules and flanked by pair of sensilla; anal opening bordered by well developed frill bearing long setular extensions.

Caudal rami (Figure 2A, B). Short, cylindrical, as long as wide; each ramus with 7 setae: seta I subventral, bare and shortest; setae II and III bare; setae IV and V bipinnate, fused basally, and with predesigned fracture planes [seta V presumably longest but incomplete in all specimens examined including holotype, *cf.* Hamond (1968: Fig. 3)]; seta VI bipinnate; seta VII tri-articulate at base. Each ramus with spinules on outer dorsal surface; additional spinular ornamentation present along inner and outer margins and around ventral and dorsal hind margins; long tube-pore present near ventral hind margin.

Antennule (Figure 2D). Seven-segmented, slender; with well developed sclerite around base of segment 1; several rows of long spinules present along posterior margins of all segments except for apical segment, and along anterior margins of segments 1–4. Segments 1–2 without spinous processes. Segment 2 largest; segment 4 with aesthetasc fused basally to seta and arising from distinct pedestal. Armature formula: 1-[1], 2-[7

+ 1 pinnate], 3-[7], 4-[1 + (1 + ae)], 5-[1], 6-[2], 7-[7 + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 2 bare setae.

Antenna (Figure 3A). Three-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with 2 rows of spinules. Allobasis not elongate; without distinct surface suture marking original segmentation but with membranous insert around base of exopod; with one abexopodal bipinnate seta in distal half. Exopod small, twice longer than width, with 4 well developed pinnate setae (2 laterally, 2 apically), distal lateral and inner distal ones with finer spinules; one row of coarse spinules on anterior surface. Endopod shorter than allobasis; lateral armature arising in distal half, consisting of one bare seta flanked by 2 strong pinnate spines; apical armature consisting of 2 strong spines and 3 geniculate setae (one geniculate seta fused basally to short seta). Endopod with 2 rows of long spinules laterally and 2 transverse hyaline frills subapically.

Labrum. Well developed; spinular ornamentation on anterior surface as in Figure 2E.

Mandible (Figure 3B). With well developed gnathobase bearing several multicuspidate teeth around distal margin and one pinnate spine at dorsal corner as in original description (Hamond 1968: Fig. 6). Palp (Figure 3B) small; endopod and exopod fused to basis, represented by small peduncles bearing 3 plumose and one pinnate seta(e), respectively. Basal armature represented by one plumose seta.

Paragnaths (Figure 2F). Strongly developed paired lobes with medially directed hair-like setules, separated by medial lobe covered by dense pattern of short setules.

Maxillule (Figure 3C). Praecoxa with few long spinules around outer margin; arthrite strongly developed, with a tube-seta on anterior surface and 8 spines/setae around distal margin; one transverse row of long spinules on posterior surface, and one row of small spinules along inner margin of arthrite. Coxa with cylindrical endite bearing a naked seta and a curved, pinnate spine; with spinular row on anterior surface. Basis with cylindrical endite bearing 2 naked setae and a pinnate spine; with several spinular rows on anterior surface. Endopod completely incorporated into basis, forming cluster of 3 plumose setae; exopod 1-segmented, with 2 plumose setae and several rows of fine spinules on surface.

Maxilla (Figure 3D). Syncoxa with 3 endites; with a row of long spinules along outer margin, several rows of spinules on posterior surface, and several spinules along inner margin; praecoxal endite small and cylindrical, with one bare seta; both coxal endites with a strong pinnate spine and 2 pinnate setae with subapical tubular extension; proximal coxal endite with one row of spinules anteriorly. Allobasis drawn out into strong, slightly curved, distally pinnate claw; accessory armature consisting of 2 pinnate and 2 naked setae. Endopod represented by one bipinnate and 3 naked setae, surrounded by spinules at base.

Maxilliped (Figure 3E). Syncoxa elongate, with 2 plumose setae and two rows of spinules. Basis with one row of spinules along outer margin, palmar margin completely bare. Endopod drawn out into long claw; with one short accessory seta anteriorly, and one tube-pore posteriorly.

Swimming legs. P1–P4 (Figures 4A, B; 5A–C). With wide intercoxal sclerites and well developed praecoxae. Praecoxae, coxae and bases with anterior rows of surface spinules as figured. Exopods 3-segmented, endopods 2-segmented.

P1 (Figure 4A). Coxa large; with several spinular rows and patches as figured. Basis with bipinnate seta on distal pedestal near insertion of endopod, long setules along inner margin and one bipinnate spine and several spinules along outer margin; anterior tube-pore near articulation with coxa. Exp-1 with one bipinnate seta; exp-2 with one naked outer seta; exp-3 with 2 virtually naked and 2 geniculate setae. Enp-1 1.8 times as long as exopod, with long spinules along proximal half of inner margin; enp-2 with one strong, minutely denticulate claw, and one small naked seta; several spinules along outer margin and around inner distal corner.

P2–P4 (Figures 4B; 5A, B). Coxae and bases with spinular rows along outer margin and on anterior surface; basis with tube-pore on anterior surface; outer margin of basis with bipinnate spine (P2) or naked seta (P3–P4); exopodal and endopodal segments with elaborate spinular/setular ornamentation as figured. P4 outer exopodal spines with long spinules. P2–P4 endopods with short enp-1 and long, inflated enp-2; outer margin of enp-2 weakly chitinized, with 2 parallel rows of flimsy setular extensions, possibly surrounding glandular structure (Figure 5B). P3–P4 enp-2 with tube-pore near distal margin. P2 enp-2 twice times longer than enp-1; endopod reaching to distal margin of exp-2; exp-3 longest. P3 enp-2 2.5 times longer than enp-1; endopod reaching to distal margin of exp-2; exp-3 longest. P4 enp-2 2.6 times longer than enp-1, posterior distal margin with spinular row (Figure 4D); endopod reaching to about distal margin of exp-2; exp-3 subequal to exp-1. Outer distal seta of P4 enp-2 clearly shorter than others; inner seta of enp-1 very long (arrowed in Figure 4B) and much longer than in P3 enp-1 (arrowed in Figure 5C). Spine and setal formulae of swimming legs as for genus.

Fifth pair of legs (Figure 6E). Baseoendopods not medially fused, with distinct medial extension. Exopod and baseoendopod discrete, each with pattern of spinules as figured; spinular pattern on exopod denser than on baseoendopod. Baseoendopod forming long, outer setophore bearing basal seta and rows of spinules; with 3 tube-pores on anterior surface; endopodal lobe just extending to proximal area of exopod, with 2 apical and 3 lateral bipinnate setae, proximal and inner middle ones minutely pinnate. Exopod elongate, about 3 times longer than wide; with one naked terminal seta, one bipinnate inner seta, and one bare and 3 pinnate setae along outer margin; terminal seta arising from short cylindrical process.

Egg-sac. Number of eggs and arrangement unknown.

Description. Male. *Body* (Figure 1C). Body length 570–587 µm (n=3; mean 579 µm). Largest width at posterior margin of cephalic shield (144 µm). Urosome narrower than prosome. Prosome (Figure 1C) 4-segmented, comprising cephalothorax and 3 free pedigerous somites. Cephalothorax with smooth posterior margin; pleural areas well developed and rounded, with lobate posterolateral angles; whole surface covered with tiny spinules as in ♀. Rostrum as in ♀. Pedigerous somites covered with minute spinules as in ♀. Urosome (Figure 1C) 6-segmented, comprising P5-bearing somite, genital somite and 4 abdominal somites. All urosomites with surface ornamentation consisting of tiny spinules dorsally and laterally; ventral surface smooth except for few rows of small spinules as in ♀; ventral posterior margin with large spinules laterally and minute spinules medially. Hyaline frills of urosomites not distinct.

Antennule (Figure 6A-C). Eight-segmented; subchirocer with geniculation between segments 5 and 6. Segments 1 and 2 with several rows of long spinules along anterior and posterior margins; without protuberances. Segment 3 (Figure 6B) with few spinules along anterior margin. Segment 4 represented by small U-shaped sclerite around anterior margin (see insert in Figure 6B). Segment 5 swollen. Segment 8 triangular (Figure 6C). Segmental homologies: 1-(I), 2-(II–VIII), 3-(IX–XII), 4-(XIII), 5-(XIV–XX), 6-(XXI–XXII), 7-(XXIII), 8-(XXIV–XXVIII). Armature formula: 1-[1], 2-[1 pinnate + 8], 3-[8], 4-[2], 5-[9 + 1 pinnate + 1 modified + (1 + ae)], 6-[3 modified spinous elements], 7-[1], 8-[8 + acrothek]. Apical acrothek consisting of minute aesthetasc and 2 naked setae.

Swimming legs. P2–P4 (Figures 4C; 5D). Shape and surface ornamentation of intercoxal sclerites and protopods as in ♀. P2–P3 enp-2 with double row of setular extensions along outer lateral margin as in ♀ (absent in P4; Figure 4C). No sexual dimorphism on P2. Endopodal segments of P3–P4 modified.

P3 (Figure 5D). Exopod as in ♀. Endopod 2-segmented, modified, not reaching to distal margin of exp-2. Enp-1 with several spinules on inner distal margin (arrowed in Figure 5D); inner seta absent. Enp-2 produced distally into short, straight, spiniform apophysis (homologous with outer spine of enp-2 in ♀; arrowed in Figure 5D) surrounded at base by row of coarse spinules.

P4 (Figure 4C). Exopod as in ♀. Endopod relatively shorter than in ♀. Enp-1 with several spinules along inner margin (arrowed in Figure 4C); inner seta absent; outer lateral margin without setular extensions found in ♀. Enp-2 twice longer than enp-1; both apical setae about equally long and longer than in ♀.

Fifth pair of legs (Figure 6D). Baseoendopods fused medially, with spinular patch medially. Baseoendopod with large setophore bearing outer basal seta; endopodal lobe vestigial bearing one pinnate and one bare seta; with one tube-pore along medial margin, and one tube-pore near articulation with exopod; with few coarse spinules at base of setophore. Exopod about twice as long as maximum width; with one inner, one apical and 2 outer setae; all setae pinnate except for distal outer one being smooth; anterior surface with several large spinules.

Sixth pair of legs (Figure 6D). Asymmetrical; represented on both sides by small plate (fused to ventral wall of supporting somite on one side; articulating at base and covering gonopore on other side; dextral and sinistral configurations observed); outer distal corner produced into cylindrical process bearing several spinules, one bipinnate inner and one naked outer seta.

Discussion. Hamond's (1968) original description of the female of *Pseudonychocamptus carthyi* is detailed by contemporary standards. Our redescription revealed some minor observational errors: (1) the entire body is covered by fine spinules instead "… a few long limp hairs, widely scattered here and there"; (2) the third antennulary segment has 7 setae instead of 5; (3) the distal lateral and inner distal setae of the antennary exopod have fine spinules instead of membranous laminae; (4) the antennary endopod has an additional subdistal spine and the outermost geniculate seta is fused at the base to a minute seta; (5) the basis and coxal endite of the maxillule have an ad-

ditional seta; (6) the maxilla has a unisetose praecoxal endite and the endopod 4 setae instead of 2; (7) the P1 displays distinct spinule rows along the outer margin of the praecoxa and coxa, and enp-2 has a minute accessory seta at the base of the claw; (8) the outer spines of P2–P3 exp-2 and -3 are bipinnate instead of smooth; and (9) the caudal ramus has 7 setae (seta I was overlooked).

The discovery of the male of *P. carthyi* provides conclusive evidence not only for the inclusion of this species in Lee and Huys' (1999) *PWPH*-clade (grouping the genera *Pilifera*, *Pseudonychocamptus*, *Weddellaophonte* and *Heteronychocamptus*) but also for its exclusion from the genus *Pseudonychocamptus*. The sexual dimorphism in swimming leg armature (the inner seta of P3–P4 enp-1 being absent in the male) unequivocally links this species to the *PWPH*-clade (Table 1). The sexually dimorphic P4 endopod, being 2-segmented in the female but reduced to a minute bisetose segment in the male, is the most significant apomorphy of the genus *Pseudonychocamptus*, however, no such reduction is displayed by the male of *P. carthyi*. This species also displays the most primitive armature on P2–P5 within the *PWPH*-clade (Table 1), lending additional support to a different generic assignment. The only other genus exhibiting two inner setae on P3–P4 exp-3 is *Weddellaophonte*, however, in *P. carthyi* two additional setae are found on P3 enp-2 (formula 321). *Pseudonychocamptus carthyi* is here fixed as the type of a new genus, *Marbefia*, gen. n., which can be defined by the following autapomorphies: (1) P2–P4 enp-2 (except P4 enp-2 in ♂) inflated, with weakly chitinized outer margin bearing two parallel rows of flimsy setular extensions, possibly surrounding a glandular structure; a similar but non-homologous structure is found on the P4 endopod of species of *Corbulaseta* Huys & Lee, 2000 (Huys and Lee 2000; Gómez and Boyko 2006); (2) P4 with sexually dimorphic setation on enp-2 (outer distal seta reduced in ♀, very long in ♂); and (3) antennule ♀ with spinules along posterior margins of segments 1–6.

Fiers (1992: 213) hinted at a relationship between *Pseudonychocamptus* and the monotypic genus *Harrietella* T. Scott, 1906 (type: *Laophonte simulans* T. Scott, 1894a) but provided no supporting evidence for this claim. Presumably his assertion was adopted from Lang (1948: 1449) who recognized a similar relationship based on the shared more or less dorsoventrally flattened body and the 2-segmented P3 endopod and 1-segmented P4 endopod in the male, in addition to the overall similarity in the maxilliped, P1 and male P3 exopod. Most *Pseudonychocamptus* species, however, do not have a dorsoventrally depressed body and the general habitus is considerably different from that of *Harrietella simulans* (T. Scott 1894a; Sars 1920b). In *Pseudonychocamptus* the P4 endopod is suppressed during development in the male but not in the female, resulting in different segmentation and setation patterns, whereas in *Harrietella* both sexes display a 1-segmented endopod and no sexual dimorphism in setation is discernible (*e.g.* Vervoort 1950; Hicks 1989). The 2-segmented P3 endopod in the male, displaying a straight spinous outgrowth on the distal segment, is indicative of a relationship with *Pseudonychocamptus*, *Pilifera*, *Inermiphonte*, gen. n. (see below) and *Marbefia*, gen. n., however, *Harrietella* does not display the sexual dimorphism

(on P3–P4 enp-1) that defines Lee and Huys' (1999) *PWPH*-clade. Although this absence is conceivably secondary as a result of the loss of the inner seta on P3 enp-1 in the female, confirmation of its membership of this clade will probably have to await the arrival of molecular sequence data. *Harrietella* is here tentatively regarded as the sistergroup of *Inermiphonte*, gen. n. (see below).

Although the mosaic distribution of unique plesiomorphies in single species [e.g. *Heteronychocamptus exiguus* (Sars, 1905) with inner seta on P2 enp-1 (*cf.* Sars 1905: Fig. 125); *Laophonte danversae* Hamond, 1969 with 5 elements on ♂ P5 exopod (*cf.* Hicks 1982: Fig. 6); *P. carthyi* with 3 inner setae on ♀ P3 enp-2 (Figure 5C)] hampers the analysis of the basal relationships within the *PWPH*-clade, a well defined group of five genera can be distinguished based on the sexual dimorphism of the P3 endopod. In males of *Marbefia*, gen. n., *Pseudonychocamptus*, *Pilifera*, *Inermiphonte*, gen. n. and *Harrietella* the ramus is 2-segmented (instead of 3-segmented), bearing a straight (rather than a sigmoid) apophysis on the outer margin of the distal endopod segment (Table 1). Within this lineage, *Marbefia* is considered to be the basal offshoot, the other four genera sharing a suite of synapomorphic reductions on the swimming legs: (1) P3–P4 exp-3 with 1 inner seta, (2) P2 enp-1 with 1 inner seta, and (3) P3 enp-2 ♀ with at most 2 inner setae.

Key to the species of *Pseudonychocamptus* Lang, 1944

Lang (1944, 1948) proposed the genus *Pseudolaophonte* for four species previously allocated to the genus *Laophonte* Philippi, 1840: *Laophonte koreni* Boeck, 1873 (type by original designation), *L. gracilis* T. Scott, 1903, *L. proxima* Sars, 1908a and *L. abbreviata* Sars, 1920a. Noodt (1952) removed *L. gracilis* and designated it as the type (by original designation) of a new genus *Pilifera* Noodt, 1952 which has remained monotypic since its proposal. New species were added to *Pseudonychocamptus* by Lang (1965: *P. paraproximus* and *P. spinifer*), Hamond (1968: *P. carthyi*), Apostolov and Petkovski (1980: *P. marinovi*), Ceccherelli (1988: *P. colomboi*) and Apostolov (2008: *P. kolarovi*).

Both Sars (1908a) and Wilson (1932) described *Laophonte proxima* on the basis of females only (the latter author from a freshwater locality!) whereas Klie (1929) provided the first illustrations of the male, including the P5 which he figured with one seta on the endopodal lobe. Lang (1965) distinguished the closely related *Pseudonychocamptus proximus* and *P. paraproximus* on the basis of morphometric differences in the distal segment of the P4 exopod and P5 baseoendopod in the female and the P5 exopod in the male. An additional differentiating character used in his key referred to the number of setae on the male P5 baseoendopod. Hamond (1968) and Ceccherelli (1988) followed Lang's judgement, however Mielke (1975), in his redescription of the male of *P. proximus*, pointed out that the latter has two setae on the P5 baseoendopod (as in all other congeners), rendering the distinctiveness of *P. paraproximus* doubtful. Although we have followed Bodin (1997) and Wells (2007) in considering the latter a species of uncertain status (here ranked as *species inquirenda*), we have nevertheless included it in the key below, based on the interspecific differences displayed in the length/width ratio of the male P5 exopod (Table 2).

Recently, Apostolov (2008) added a new species, *P. kolarovi*, based on two males collected from the Kavala beach (Greece) in the Aegean Sea. The author claimed that the species occupied an isolated position in the genus on account of the structure of the caudal rami and P1–P5. The 2-segmented P4 endopod (with one inner and two distal setae), the presence of 5 setae on the P5 exopod and the sexually dimorphic distal inner spine on the P2 endopod clearly exclude *P. kolarovi* from the genus *Pseudonychocamptus* and particularly the latter character unequivocally points to a relationship with the genera *Paralaophonte* Lang, 1944 and *Loureirophonte* Jakobi, 1953. The species is here formally placed in the genus *Paralaophonte* as *Paralaophonte kolarovi*, comb. n. (see below). The six valid species currently recognized in the genus, and the problematic species *P. paraproximus*, can be differentiated by the key below and the character states tabulated in Table 2.

1. P3 enp-2 with 4 setae in ♀ and 2 setae in ♂ **2**
– P3 enp-2 with 5 setae in ♀ and 3–4 setae in ♂ **3**
2. P5 exopod ♀ at least twice longer than wide, with 5 setae; P5 exopod ♂ with straight outer margin ..... ***P. koreni*** [a]
– P5 exopod ♀ about 1.3 times longer than wide, with 6 setae; P5 exopod ♂ with convex outer margin ..... ***P. spinifer***
3. Caudal ramus longer than wide **4**
– Caudal ramus wider than long ..... ***P. marinovi***
4. P5 exopod ♀ with 1 naked and 5 pinnate setae; P2 enp-2, P3 enp-2 and P5 exopod of ♂ with 4 setae **5**
– P5 exopod ♀ with 6 naked setae; P2 enp-2, P3 enp-2 and P5 exopod of ♂ with 3 setae ..... ***P. colomboi***
5. Body elongate, length 3–4 times maximum width of cephalothorax; all setae of P5 exopod ♀ marginal **6**
– Body short, length about 1.85 times maximum width of cephalothorax; P5 exopod ♀ with 4 marginal and 2 surface setae ..... ***P. abbreviatus***
6. P5 exopod ♂ about 2.7 times longer than wide ..... ***P. proximus***
– P5 exopod ♂ about 3.25 times longer than wide ..... ***P. paraproximus***

Proposal of *Inermiphonte*, gen. n.

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The taxonomic position of *Laophonte danversae* Hamond, 1969 has been surrounded by controversy since its original description. Hamond (1969) suggested a close rela-

a Chislenko's [1967 – reproduced in Kornev and Chertoprud (2008)] female from the White Sea shows a P5 exopod ♀ with length/width ratio 1.64 and a P1 endopod which is distinctly more slender than in Sars' (1908a) material; this record is considered doubtful and may well refer to another as yet undescribed species.

Table 2. Setal number and morphometric differences between species of *Pseudonychocamptus* (CR = caudal ramus; exp = exopod; enp = endopod; benp = baseoendopod). Length/width ratios based on Chislenko (1967)[a], Sars (1908a)[b], Sars (1920a)[c], Lang (1965)[d], Letova (1982)[e], Apostolov and Petkovski (1980)[f] and Ceccherelli (1988)[g].

species		P2 enp	P3 enp	P5			P5 exp ♀ L/W	CR L/W
				exp		benp		
P. koreni	♀	0.220	1.121	5		5	1.64[a]–2.36[b]	1.36[b]
	♂	0.220	0.020	4		2	–	–
P. proximus	♀	0.220	1.221	6		5	1.64[b]	1.80[b]
	♂	0.220	0.220	4		2	–	–
P. abbreviatus	♀	0.220	1.221	6		5	1.25[c]	1.38[c]
	♂	0.220	0.220	4		2	–	–
P. paraproximus	♀	0.220	1.221	6		5	1.44[d]	1.65[d]
	♂	0.220	0.220	4		2	–	–
P. spinifer	♀	0.220	1.121	6		5	1.22[d] –1.27[e]	1.14[e] –1.23[d]
	♂	0.220	0.020	4		2	–	–
P. marinovi	♀	0.220	1.221	6		5	2.1[f]	0.85[f]
P. colomboi	♀	0.220	1.221	6		5	1.84[g]	1.12[g]
	♂	0.120	0.120	3		2	–	–

tionship with *L. cesareae* Por, 1964 (currently placed in *Loureirophonte*; *cf.* Fiers 1993 – see below) without giving any compelling evidence for this affiliation. Although his description of *L. danversae* was based solely on females from West Runton the author also illustrated a single male from the same locality under the nondescript name "Laophontid male, ?gen., ?sp.". Hamond (1969) suggested that the latter might have been the unknown male of *L. danversae*, were it not for the marked differences observed in the rostrum, caudal rami and the armature on the P2–P4 exopods. In an addendum to his paper he also remarked that "Laophontid male, ?gen., ?sp." and the male of *Laophonte* ?*drachi* Médioni & Soyer, 1966 shared the same type of sexual dimorphism on the P3 endopod and that the latter species was obviously closely related to *L. danversae*. As pointed out by Hicks (1982), Bodin (1971) clearly misinterpreted Hamond's remarks when he suggested conspecificity between *L. danversae* and *L.* ?*drachi*. This misconception was perpetuated in the literature by Wells (1976) who considered Hamond's "Laophontid male, ?gen., ?sp." the true male of *L. danversae* and subsequently by Bodin (1979) who regarded both female and male *L. danversae* as junior synonyms of *L.* ?*drachi*. The issue of the unknown male of *L. danversae* was finally resolved by Hicks (1982) who provided its first description based on material from Robin Hood's Bay (England). Hicks demonstrated that Hamond's (1969) "Laophontid male, ?gen., ?sp." and the males of *L. danversae* and *L.* ?*drachi* were significantly different in the swimming legs, leg 5 and caudal rami, corroborating their distinct specific identity but his comparative analysis did not, however, contribute

anything new to elucidating the relationships of this species group within the Laophontidae. Hamond (1969) had previously suggested that *L. danversae* might best be classified as an "anomalous species" of *Laophonte*, which does not fit into any of the species groups proposed by Lang (1948). Médioni and Soyer (1966) tentatively assigned *L.* ?*drachi* to the *inopinata*-group of *Laophonte* and noted some similarities with *L.* ?*platychelipusoides* Noodt, 1958 (currently placed in *Coullia* Hamond, 1973; *cf.* Hamond 1973; Huys 2009a). Lee and Huys (1999) instead recognized a relationship between *L. danversae* and the laophontid genera that display a similar type of setal sexual dimorphism on the endopods of P3–P4 (Table 1) but neither formally included the species in the *PWPH*-clade or removed it from its floating status in the genus *Laophonte*. *Laophonte danversae* is here fixed as the type species of a new genus *Inermiphonte*, gen. n. which also includes Hamond's (1969) "Laophontid male, ?gen., ?sp.". *Inermiphonte* is provisionally regarded as the sistergroup of *Harrietella* based on the following synapomorphies: (1) P2–P4 exp-3 ♀/♂ without inner setae, (2) P4 exp-2 without inner seta (exp-2 not expressed in *Harrietella* but inner margin of distal exopod segment without inner setae), (3) P3 enp-1 ♀ without inner seta, (4) P3 enp-2 ♀ with 0–1 seta, and (5) P4 enp-2 ♀ without inner setae.

Diagnosis. Laophontidae. Body linear or dorsoventrally depressed. Posterior margins of abdominal somites usually with spinule rows dorsally and ventrally. Rostrum delimited at base; broadly triangular, prominent. Genital double-somite ♀ with lateral incisions and ventrolateral internal chitinous ribs marking original segmentation. Pleural extensions of ♀ abdominal somites moderately developed. Caudal ramus rectangular or conical, longer than wide; inner margin with spinules; with 7 setae; setae IV and V well developed, pinnate; seta VI reduced, setiform. Anal operculum finely spinulose or smooth.

Sexual dimorphism in antennule, P3 (and occasionally P4) endopods, P5, P6 and in genital segmentation.

Antennule relatively short and 6- or 7-segmented in ♀; 6- or 7-segmented and (sub)chirocer with 1–2 segments distal to geniculation in ♂; segments with spinular ornamentation along anterior margin of segments 1–4 in ♀ and 1–3 in ♂; segments 1–2 without processes; dorsal surface of segment 1 with 2 thick pinnate spines; with aesthetasc on segment 4 (♀) or 5 (♂). Antenna with 4 setae on exopod; allobasis with abexopodal seta. Mandibular palp elongate, 1-segmented; with one basal, one exopodal and 3 endopodal setae. Maxillule with defined exopod bearing 2 setae. Maxilla with 3 endites on syncoxa; endopod represented by 3 setae. Maxilliped elongate; syncoxa with 2 setae; basis without distinct ornamentation; endopodal claw long and curved, with one accessory seta.

P1 long, with elongate coxa and basis; with 2- or 3-segmented exopod, distal exopod segment with 2 short and 2 geniculate setae; endopod stout, enp-1 without inner seta, enp-2 with minute seta and long minutely denticulate claw. Swimming legs P2–P4 with 3-segmented exopods and 2-segmented endopods. P2–P4 exp-3 and P4 enp-2 without inner setae; inner seta of P4 enp-1 occasionally present in ♀ but always absent in ♂. P3 enp-2 produced into straight spiniform apophysis in ♂ (homologous with

outer spine of enp-2 in ♀). Inner distal seta of P2–P4 exp-3 reduced in ♂. Armature formula of swimming legs 2 to 4 (P2–P4) as follows:

	Exopod	Endopod
P2	0.(0–1).023	0.(1–2)20
P3	0.(0–1).023	0.(0–1)21 [0.(0–1)20 in ♂]
P4	0.1.02(2–3)	(0–1).021 [0.021 in ♂]

P5 with separate exopod and baseoendopod. Exopod ovoid or elongate with 6 setae in ♀ and 4–5 setae in ♂. Endopodal lobe well developed in ♀, subtriangular, with 4–5 setae. Baseoendopods fused medially in ♂; endopodal lobes rudimentary, with 2 setae each.

P6 forming well developed operculum with 2 small setae in ♀; asymmetrical in ♂ (with dextral or sinistral configuration), with outer distal corner produced into process bearing 2 well developed elements.

Type species. *Laophonte danversae* Hamond, 1969 = *Inermiphonte danversae* (Hamond, 1969), comb. n.

Other species: *Inermiphonte hamondi,* sp. n.

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Species *incertae sedis.* *Laophonte* ? *drachi* Médioni & Soyer, 1966 = *Inermiphonte drachi* (Médioni & Soyer, 1966), comb. n.

Etymology. The generic name refers to the absence of inner setae on P2–P4 exp-3 and P4 enp-2 (Table 1). Gender: feminine.

Following Hicks' (1982) comparative analysis Hamond's (1969) "Laophontid male, ?gen., ?sp." is here assigned to a new species *Inermiphonte hamondi*, sp. n., which can be differentiated from the type species by the characters listed in Table 1 and Hicks' (1982: 306) Table II. *Laophonte* ?*drachi* shows some important differences with the other two species such as the 6-segmented antennule in the female, the 2-segmented P1 exopod, the reduced inner distal setae on the female P2–P4 exp-3 (a character typical for male *Inermiphonte*), and the presence of three strong spines on the male P4 endopod. *L.* ?*drachi* resembles *I. danversae* in the presence of only one inner seta on P2 enp-2, no inner setae on ♂ P3 enp-2 and only three outer spines on P4 exp-3; it is similar to *I. hamondi* in the presence of only four elements on the male P5 exopod. It is here placed as *species incertae sedis* in *Inermiphonte* as *I. drachi*, comb. n.

Inermiphonte danversae is thus far known only from two localities in England. Hamond (1969) recorded three females from the shore at West Runton (Norfolk) and Hicks (1980, 1982) reported the species from a range of littoral algae in Robin Hood's Bay (North Yorkshire) where it attained highest densities on *Corallina officinalis* L. and *Cladophora rupestris* (L.) Kutz. *Inermiphonte hamondi* and *I. drachi* are known only from their respective type localities, the former from the intertidal zone at West Runton (Hamond 1969) where it may co-exist with *I. danversae*, the latter from colonies of the bryozoan *Schismopora armata* (Hincks, 1860) near Racou (Roussillon, France) (Médioni and Soyer, 1966).

Key to the species of *Paralaophonte* Lang, 1948

Included species: *Paralaophonte pallaresae,* sp. n.
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The genus-group name *Paralaophonte* was first published by Lang (1944) who subdivided the genus in four species-groups and designated a type species for three of them: (1) *brevirostris*-group (no type designated), (2) *perplexa*-group (type: *Laophonte perplexa* T. Scott, 1899), (3) *gracilipes*-group (type: *Laophonte gracilipes* Brady, 1910), and (4) *karmensis*-group (type: *Laophonte karmensis* Sars, 1911). The artificiality of this system was subsequently exposed by the discovery of "transitionary" species which blurred the boundaries of some of the species groups (*e.g.* Vervoort 1962); consequently, Lang's (1944, 1948) subdivision was finally disposed off by Wells (2007). Vervoort (1964) remarked that *Paralaophonte* Lang, 1944 is an unavailable generic name which was subsequently validated by Lang (1948) by the indication of a type species (*Cleta brevirostris* Claus, 1863) and the provision of an accompanying generic diagnosis. The authorship and date of this genus should, therefore, be attributed as *Paralaophonte* Lang, 1948 (Huys 2009b).

According to the latest checklist (Wells 2007), the genus *Paralaophonte* currently includes 33 valid species and one *species incertae sedis* (*Laophonte lamellipes* Nicholls, 1944). Various authors (*e.g.* Willey 1935; Nicholls 1945; Yeatman 1970; Hamond 1973; Wells and Rao 1987; Wells 2007) have commented on the difficulties in separating the two most widely distributed species, *P. brevirostris* (Claus, 1863) and *P. congenera* (Sars, 1908b), and some of them have casted doubt on the validity of this separation. Both species have also been reported to display a great deal of variability in the rostrum, antennule, leg 5 and caudal rami (*e.g.* Wells and Rao 1987) but it is unclear to what degree this pertains to genuine intra- or interpopulation variability or whether this is a reflection of allopatric or sympatric closely related species (as hinted at by Mielke 1981). The further subdivision of both species in subspecies has also led to taxonomic confusion. For example, Willey's (1935) variety "*fissirostris*" of *P. brevirostris* was upgraded to subspecies level by Lang (1965) (and accepted by most subsequent authorities: *e.g.* Wells et al. 1982; Wells 2007) but allegedly differs from the nominotypical subspecies only in the shape of the rostrum. Given the reported variability in this structure in other species it seems impractical to maintain Willey's (1935) subspecies at present and hence they are here formally declared invalid. Similarly, *P. congenera mediterranea* Lang, 1948 appears to be more closely related to *P. lacerdai* Jakobi, 1953 than to its nominotypical subspecies *P. congenera congenera*. In fact both taxa can only be separated by subtle differences in the caudal ramus, length of endopodal setae in the female P5 and shape of the endopodal margin in the male P5. Likewise, *Paralaophonte pacifica galapagoensis* Mielke, 1981 is more similar to *P. brevirostris* than to its nominotypical subspecies *P. pacifica pacifica* Lang, 1965 (see also Wells 2007); the first two taxa differ primarily in details of the female antennule, P4 endopod and the male P3 exopod. Mielke's (1981) subspecies is here upgraded to full species rank since it differs sufficiently from Lang's (1965) population to warrant such status: (a) second antennulary segment with blunt protuberance instead of spinous projection; (b) P1 enp-1 10

times instead 8 times as long as wide; (c) P2–P3 exopods ♀ distinctly shorter; (d) P3 exp-3 ♂ inner distinctly longer instead of shorter than outer distal spine; (e) baseoendopod P5 ♂ with strongly developed seta instead of tiny reduced seta; and (f) caudal ramus 1.3 times as long as maximum width instead of quadratic.

Brady's (1910) original description of *P. gracilipes* (as *Laophonte gracilipes*) from the Kerguelen Islands (Grande Terre, Baie de l'Observatoire) is fragmentary and lacking in detail. Lang (1936) redescribed the species based on material from the Falklands and Pallares (1968) did the same using material from Puerta Deseado (Santa Cruz, Argentina). However, both redescriptions differ significantly in the number of inner setae on P3–P4 exp-3, the morphology of the female P5, the size of P1 exopod (relative to the endopod) and the length of the apophysis on the male P3, strongly suggesting that the Falklandian and Argentinian populations belong to different species. Wells et al. (1982) and Wells (2007) adopted Lang's (1936) swimming leg armature pattern in their respective identification keys, however, both incorrectly stated that the male P5 endopodal lobe lacked setae. Although Lang (1936) showed an endopodal seta, their error presumably stemmed from a misinterpretation of Brady's (1910) original figure of the male P5 which also shows the endopodal seta but not the typical outer basal one. Although the supporting evidence is admittedly slim (morphometric differences in P1 exopod and P2 endopod ♂) we have elected to attribute the Falklandian material to *P. gracilipes* and to propose a new species, *P. pallaresae*, sp. n., for the specimens illustrated by Pallares (1968). It should be noted that Pallares figured the female antennule as 8-segmented but stated in the text that it consists of only 7 segments (which is conceivably the correct number). *Paralaophonte obscura* Vervoort, 1962 from New Caledonia appears to be most closely related to *P. pallaresae*, sp. n. but differs from the latter in the female by the presence of a small conical protuberance on the second antennulary segment and the semicircular P5 exopod in which the inner distal seta is only slightly longer than proximal inner one, and in the male by the presence of only 4 elements on the P5 exopod. *Paralaophonte pallaresae*, sp. n. can be characterized by the following differential diagnosis:

Paralaophonte. Abdominal somites without a middorsal spinous process. Caudal rami cylindrical, about 1.5 times as long as maximum width; with seta V elongate. Antennule ♀ 7-segmented; segment 2 without horn, spinous process or protuberance. P1 exopod 3-segmented. P3–P4 exp-3 with 1 inner seta. P3 enp-2 ♀ with 5 elements. P3 endopod ♂ 3-segmented with apophysis on enp-2 and 4 elements on enp-3; apophysis distinctly longer than endopodal segments combined. P4 enp-2 with 4 elements. P5 exopod ♀ longer than wide, inner distal seta twice the length of proximal inner one; baeoendopod with 4 elements. P5 exopod ♂ with 5 elements; longest seta at most 2.5 times the length of segment; endopodal margin with 1 long seta. Body length: 590–670 µm (♀), 500–510 µm (♂).

The original material collected by Dr Rosa Pallares is no longer available for re-examination (Dr S. Ménu-Marque, Universidad de Buenos Aires, pers. commn). In accordance with ICZN Arts 16.4 and 72.5.6 the male specimen illustrated by Pallares (1968: 87) in her plate XXXII (Figs 1, 5, 9, 12, 15) is here fixed as the holotype of *P. pallaresae*, sp. n. Type locality: Puerto Deseado, Santa Cruz Province (Argentina), plankton.

Jakobi (1953) proposed the genus *Loureirophonte* for two new species from Southern Brazil, *L. catharinensis* (type by original designation) and *L. paranaensis* and claimed a close relationship with the *inopinata*-group of *Laophonte*. Both Vervoort (1964) – who favoured a relationship with the *inornata*-group of *Laophonte* – and Lang (1965) questioned the accuracy of Jakobi's illustrations and generic diagnosis and doubted the validity of *Loureirophonte* until Mielke (1981) confirmed its separate identity by providing a detailed description of a third species, *L. isabelensis* Mielke, 1981. This course of action was corroborated by Fiers (1993) in his revision of the genus which saw the addition of five new species and another two which were transferred from other genera (*Laophonte caesarea* Por, 1964; *Paralaophonte subterranea* Lang, 1965). With the recent addition of *L. psammophila* Mielke, 2001 and *L. minutum* Gómez & Boyko, 2006 the genus now includes 12 species (Mielke 2001; Gómez and Boyko 2006) (Table 3) although it is known that other as yet undescribed species occur in the Galapagos (Mielke 1981). Fiers (1993) provided a key to species which was recently updated by Gómez and Boyko (2006). Fiers was also the first to claim a sistergroup relationship between *Paralaophonte* and *Loureirophonte* based on the sexual dimorphism of the P2 endopod, the presence of 5 setae on the P5 exopod of both sexes, and the presence of 4 setae and one seta on the P5 endopodal lobe in females and males, respectively. He also listed a suite of characters that serves to distinguish *Loureirophonte* from its sistertaxon: (a) P2 enp-2 ♀ with 1 distal and 2 inner setae (0.210); (b) bulbous appearance of the sexually dimorphic distal inner seta of P2 enp-2 (with a lamellar structure in the distal third); and (c) 1-segmented P4 endopod. Characters (a) and (c) are autapomorphies of *Loureirophonte* (although Fiers (1993) did report specimens of *L. mediterranea* that displayed a 2-segmented P4 endopod) supporting the monophyly of the genus. Both *Paralaophonte* and *Loureirophonte* display a homologous sexual dimorphism on the P2 endopod, involving the modification of the distal inner seta on enp-2. In the former genus the seta has attained a further derived state of modification (as described under character (b) above), raising the suspicion that *Loureirophonte* is merely nested within *Paralaophonte*. Indeed, at present there is not a single apomorphy supporting the monophyly of *Paralaophonte*, potentially rendering the latter paraphyletic exclusive of *Loureirophonte*. In addition, the dichotomy between the two genera that was traditionally based on different types of P2 endopod sexual dimorphism appears to be false since it is neither jointly exhaustive nor mutually exclusive. The evolutionary transition between both genera is best demonstrated by the modification in male *Paralaophonte macera* Sars, 1908b and *P. asellopsiformis* Lang, 1965 which is virtually identical to the *Loureirophonte* condition and, similarly, the state of the inner distal seta in male *L. furcata* Fiers, 1993 which resembles the *Paralaophonte* condition (Sars 1908b; Fiers 1993). Although the presence of such intermediate taxa casts further doubt on the validity of the basal split between *Loureirophonte* and *Paralophonte* we have refrained from synonyzing these genera pending a thorough phylogenetic analysis at species level.

Five species have been added to the genus *Paralaophonte* since Wells' (2007) checklist: *P. lamellipes* (Nicholls, 1944), comb. n., *P. galapagoensis* Mielke, 1981, grad. n.,

Table 3. Differentiating characters of *Paralaophonte* and *Loureirophonte* species [A1 = number of antennulary segments in ♀; Pr = protuberance on second antennulary segment (– : absent; +: small conical or blunt protuberance; s: straight spinous process; H: prominent, recurved, unguiform process); P1 (exp = number of exopodal segments; sd = number of setae/spines on distal exopodal segment); P3 enp ♂ = armature formula with A indicating precense of apophysis on middle segment; ? = unknown].

Paralaophonte Lang, 1944	A1	Pr	P1		P2		P3		P4		P5 ♀		P5 ♂		P3 enp ♂
			exp	sd	exp	enp	exp	enp	exp	enp	exp	benp	exp	benp	
P. brevirostris (Claus, 1863) [a]	6	+	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
P. meinerti (Brady, 1899)	7	s	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
P. congenera congenera (Sars, 1908b) [b]	7	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
P. congenera mediterranea Lang, 1948	7	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	4	1	0.A.220
P. lacerdai Jakobi, 1953	7	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	4	1	0.A.220
P. royi (Jakubisiak, 1932)	6	+	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
P. octavia (Monard, 1935) [c]	7	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	?	?	?
P. dieuzeidei (Monard, 1936)	6	H	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
P. gurneyi (Lang, 1934) [d]	7	s	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	6	4	5	1	0.A.220
P. majae Petkovski, 1964	6	+	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	5	5	1	0.A.220
P. asellopsiformis Lang, 1965	6	H	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
P. pacifica Lang, 1965	6	s	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
P. galapagoensis Mielke, 1981, grad. n.	6	+	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
P. ormieresi Raibaut, 1969	6	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	4	4	5	1	0.A.220
P. septemarticulata Chislenko, 1978	7	s	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	4	4	?	?	?
P. perplexa (T. Scott, 1899)	7	–	2	5	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	0	0.221
P. hyperborea (Sars, 1909) [e]	7	–	2	5	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	0	0.A.220
P. pilosoma Vervoort, 1964 [f]	?	H	2	5	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	?	?	5	1	0.A.220
P. macera (Sars, 1908b) [g]	7	+	2	5	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	5	0	0.A.120
P. sculpta Hamond, 1973 [h]	7	–	3	4	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	?	?	?
P. problematica Mielke, 1981	6	s	3	4	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	5	1	0.A.220
P. echinata Fiers, 1986	6	–	3	4	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	5	1	0.A.220
P. gracilipes (Brady, 1910)	7	–	3	4	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	5	1	0.A.220

Paralaophonte Lang, 1944	A1	Pr	P1		P2		P3		P4		P5 ♀		P5 ♂		P3 enp ♂
P. innae Chislenko, 1977 [i]	7	–	2	5	0.1.123	0.220	0.1.223	0.320	0.1.223	0.121	5	4	5	0	0.320
P. panamensis Mielke, 1982	6	+	2	5	0.1.123	0.220	0.1.223	0.321	0.1.222	0.121	5	4	5	1	0.A.220
P. harpagone Gheerardyn, Fiers, Vincx & De Troch, 2006	6	+	2	4	0.1.123	0.220	0.1.223	0.220	0.1.222	0.120	4	4	5	1	0.220
P. taurina (Monard, 1928)	7	H	3	4	0.1.123	0.220	0.1.223	0.320	0.1.123	0.121	5	5	?	?	?
P. longipes (T. Scott, 1894b	7	–	2	5	?	?	0.1.123	0.321	?	?	5	3	?	?	?
P. karmensis (Sars, 1911) [j]	7	+	2	5	0.1.123	0.220	0.1.123	0.321	0.1.123	0.121	4	4	5	1	0.A.220
P. tenera (Sars, 1920a)	7	+	2	5	0.1.123	0.220	0.1.123	0.321	0.1.123	0.121	5	4	4	1	0.A.120
P. lunata (Willey, 1930)	7	–	2	5	0.1.123	0.220	0.1.123	0.321	0.1.123	0.121	5	4	5	1	0.A.220
P. spitzbergensis Mielke, 1974	7	+	2	5	0.1.123	0.220	0.1.123	0.321	0.1.123	0.121	5	4	5	0	0.A.220
P. zimmeri (Douwe, 1929)	6	+	3	4	0.1.123	0.220	0.1.123	0.321	0.1.123	0.121	5	4	5	1	0.A.220
P. obscura Vervoort, 1962	7	+	3	4	0.1.123	0.220	0.1.123	0.221	0.1.123	0.121	5	4	4	1	0.A.220
P. pallaresae, sp. n.	7	–	3	4	0.1.123	0.220	0.1.123	0.221	0.1.123	0.121	5	4	5	1	0.A.220
P. quaterspinata (Brian, 1917) [k]	6-7	–	3	4	0.1.123	0.220	0.1.123	0.220	0.1.123	0.121	5	2	5	1	0.220
P. livingstoni Apostolov, 2004	7	+	3	4	0.1.123	0.220	0.1.123	0.220	0.1.123	0.120	5	4	?	?	?
P. kolarovi (Apostolov, 2008) comb. n. [l]	?	–	3	4	0.1.123	0.220	0.1.123	0.?20	0.1.123	0.120	?	?	5	1	0.220
P. aenigmaticum Wells, Hicks & Coull, 1982	6	–	2	5	0.1.123	0.220	0.1.123	0.320	0.1.022	0.120	5	3-4	4	1	0.220
P. lamellipes (Nicholls, 1944) [m]	7	–	2	5	0.1.122	0.220	0.1.222	0.220	0.1.222	0.120	5	4	5	0	0.220
Loureirophonte Jakobi, 1953															
L. minutum Gómez & Boyko, 2006	?	–	2	5	0.1.023	0.210	0.1.023	0.020	0.1.022	1	?	?	5	1	0.020
L. isabelensis Mielke, 1981	6	+	2	5	0.1.023	0.210	0.1.023	0.120	0.0.022	110	5	4	5	1	0.120
L. furcata Fiers, 1993 [n]	?	+	2	5	0.1.023	0.210	0.1.023	0.120	0.0.022	110	?	?	5	1	0.120
L. catharinensis Jakobi, 1953 [o]	6	+	2	5	0.0.023	0.210	0.0.023	0.120	0.0.022	110	5	4	5	1	0.120
L. paranaensis Jakobi, 1953 [o, p]	6	+	2	5	0.0.023	0.210	0.0.023	0.120	0.0.022	110	5	4	5	1	?
L. cesareae (Por, 1964)	6	+	2	5	0.1.023	0.210	0.1.023	0.020	0.0.023	010	5	4	5	1	0.020
L. mediterranea Fiers, 1993 [q]	6	+	2	5	0.1.023	0.210	0.1.023	0.020	0.0.023	010	5	4	5	1	0.020
L. majacola Fiers, 1993	6	+	2	5	0.0.023	0.210	0.0.023	0.020	0.0.023	010	5	3	5	1	0.020

Loureirophonte Jakobi, 1953															
L. subterranea (Lang, 1965) [r]	6	–	2	5	0.0.012	0.(1-2)10	0.0.012	0.(1-2)20	0.0.022	020	4	4	5	1	0.120
L. laingensis Fiers, 1993	6	+	2	5	0.0.023	0.210	0.0.023	0.120	0.0.022	110	5	4	5	1	0.120
L. majahualensis Fiers, 1993	6	+	2	5	0.0.023	0.210	0.0.023	0.120	0.0.022	110	5	4	5	1	0.120
L. psammophila Mielke, 2001	6	+	2	5	0.1.022	0.210	0.1.022	0.120	0.0.022	010	5	4	5	1	0.120

[a] Wells and Rao (1987) also recorded specimens with a 7-segmented antennule in the female and without a spur on the second segment; Hamond (1972) also observed the 7-segmented condition while Petkovski (1964) recorded a female with a 6-segmented antennule without a spur on the second segment. According to Wells and Rao (1987) the shape and size of the rostrum and the cephalothorax remains as the only reliable criterion to distinguish *P. brevirostris* from *P. congenera*. Pending a re-examination of topotype material, Willey's (1935) variety *fissirostris*, which was upgraded to subspecific level by Lang (1965), is no longer recognized as valid.

[b] Sars' (1908b) original description of the male shows 2 setae on the P5 baseoendopod; re-examination of the type material revealed that the short inner element represents a tube-pore. Both Hamond (1972, 1973) and Wells and Rao (1987) pointed out the difficulties in discriminating *P. congenera* and *P. brevirostris*. Hamond's (1969) male shows a spur on the second segment of the antennule [also present in the North Carolina material examined by Hamond (1973)] and a distinctly pitted cephalothorax; Sars (1908b) did not observe these characters in the Norwegian material. Yoo and Lee's (1995) record from the Yellow Sea displaying only 4 setae on P5 exopod ♂, appears to represent a different species; Wells (2007) pointed out that their illustration of the P4 in reality refers to the P2.

[c] Monard's (1935) report of an 8-segmented antennule in this species is considered unlikely (*cf.* Lee and Huys 1999). The species was originally described from Salammbô (Tunisia) and has not been recorded again until recently when Nurul Huda and Zaleha (2005) found it in Peninsular Malaysia; their record (and that of Zaleha et al. 2006) which gives only the armature formula of P2–P4 requires confirmation. Goddard's (2006) claim that his material from Robinson Crusoe Island (Juan Fernández Archipelago, Chile) may be attributed to *P. octavia* cannot be substantiated because it displays only one inner seta on P3–P4 exp-3; the only other known species which displays the same reduced formula is *P. zimmeri* but this species has a 6-segmented antennule in the female and a small spinous process on its second segment [8-segmented (?) and without such process in Goddard's material].

[d] Both Gurney (1927) and Sewell (1940) erroneously illustrated the female antennule as 8-segmented (*cf.* Lee and Huys 1999: 324).

[e] Kornev and Chertoprud's (2008) swimming leg armature formula for this species is radically different from that mentioned in previous descriptions (Sars, 1909; Mielke, 1974): P2 (exp: 0.1.123; enp: 1.120), P3 (exp: 0.1.223; enp: 0.221), P4 (exp: 0.0.023; enp: 0.121). The reported absence of the spur on the second antennulary segment requires confirmation.

[f] Vervoort (1964) reported a very long inner seta on P3 enp-2 in the male but re-examination of the holotype has proven this to be erroneous (Huys and Lee 2000).
[g] Kornev and Chertoprud (2008) confirmed the presence of a small spur on the second antennulary segment of the female [overlooked in Sars' (1908b) original description and Chislenko's (1967) redescription]; their swimming leg armature given on p. 311 contradicts the illustrations of P2 and P4.
[h] Although Hamond (1973) showed no hesitation in placing *P. sculpta* in the *gracilipes*-group of *Paralaophonte*, its generic assignment remains doubtful because of the absence of males.
[i] Chislenko (1977) did not figure the male P3 or P4, suggesting there is no sexual dimorphism in these legs; if this proves to be correct *P. innae* is sufficiently different from *P. perplexa* to warrant distinct species status, however, females of these two species may be extremely difficult to separate.
[j] Chislenko's (1967) specimens from the White Sea differ from Sars' (1911) type population in several aspects and may represent a distinct species: (1) second antennulary segment ♀ without a spur; (2) P5 exopod ♀ with 5 elements instead of 4; (3) P2 enp-2 ♂ distinctly longer; (4) P3 exp-1 ♂ outer spine much larger; (5) P3 exp-3 ♂ with only 1 inner seta instead of 2; and (6) P5 exopod ♂ and its middle element distinctly longer. Unfortunately, Kornev and Chertoprud's (2008) report on *P. karmensis* from the White Sea did not resolve the issue but instead added to the confusion surrounding it. They confirmed the presence of the antennulary spur but presented a radically divergent armature formula for P1 (exopod 3-segmented), P3 (exp: 0.1.123; enp: 0.121) and P4 (exp: 0.0.123) and considered the number of setae on the P5 exopod ♀ variable (4 or 5).
[k] There is considerable confusion over the segmentation pattern of the female antennule. Brian (1921) described it as 5-segmented with segments 1–2 partially fused; Brian (1917) and Pesta (1959) as 6-segmented; and Lang (1948) as indistinctly 7-segmented with segments 5–6 incompletely separated (based on Monard's (1928) redescription).
[l] Apostolov (2008) shows 2 inner and 2 distal setae on P3 enp-2 ♂ (formula 220); the 2-segmented condition and absence of an apophysis suggest that the outer spine is lacking in the female (as in *e.g. P. innae*); the number of inner setae expressed in *P. kolarovi* females may be 2 or 3 (in the latter case one seta is typically lost in male *Paralaophonte*).
[m] Nicholls (1944) stated that the P1 exp is 2-segmented, the distal two segments being fused with only 3 terminal setae (in reality the distal segment bears 5 elements); Huys and Lee (2000: 81) confirmed the true nature of the modified male P2 endopod and suggested a relationship with *Paralaophonte*; Wells (2007: 64) placed it as *species incertae sedis* in this genus; it is here formally transferred to *Paralaophonte* as *Paralaophonte lamellipes* (Nicholls, 1944) comb. nov. Lee and Huys (1999: 324) also confirmed that the female antennule is 7-segmented instead of 8-segmented.
[n] The modified inner distal seta resembles more the condition in *Paralaophonte* (Fiers 1993: Fig. 2c).
[o] Setal formula as reinterpreted by Fiers (1993).
[p] Fiers (1993) doubted the presence of an outer seta on P3 enp-2 and P4 endopod; these "elements" are here reinterpreted as ornamental spinules.
[q] Fiers (1993) also reported specimens with a 2-segmented P4 endopod (formula 0.010).
[r] The inner setae of P2 enp-2 are displaced towards the apical margin of the segment creating the impression that there are 1 inner and 2 distal setae instead of 2 inner and 1 distal setae; taking into account the observed variability Lang (1965) erroneously tabulated the setal formula as 0.(0–1)20; Fiers' (1993) formula [0.(1–2)20] is equally incorrect (his Table 1).

P. harpagone Gheerardyn, Fiers, Vincx & De Troch, 2006, *P. kolarovi* (Apostolov, 2008), comb. n. and *P. pallaresae*, sp. n. Although Wells (2007) listed *Laophonte royi* Jakubisiak, 1932 only as a *species incertae sedis* in the Laophontidae it is here included as a valid species of *Paralophonte*, being very closely related to *P. majae* Petkovski, 1964. The 39 species currently recognized as valid in the genus *Paralaophonte* can be identified with the key below.

1. Caudal rami broadly lamellar, close together, with seta V very short **2**
– Caudal rami usually cylindrical, with seta V elongate **3**
2. P1 exopod 2-segmented; P3 exp-3 with 1 inner seta; P4 exp-3 with 7 setae/spines; P3 exopod ♂ 2-segmented; P5 exopod ♂ with 4 spines ..... ***P. aenigmaticum***
– P1 exopod 3-segmented; P3 exp-3 with 2 inner setae; P4 exp-3 with 4 setae/spines; P3 exopod ♂ 3-segmented; P5 exopod ♂ with 5 setae ..... ***P. asellopsiformis***
3. P1 exopod 2-segmented, with 4 setae on exp-2; maxillipeds very large and specialized ..... ***P. harpagone***
– P1 exopod 3-segmented with 4 setae on exp-3, or 2-segmented with 5 setae on exp-2 ..... **4**
4. P3 exp-3 with 1 inner seta **5**
– P3 exp-3 with 2 inner setae **15**
5. P4 enp-2 with 3 elements (formula 120) **6**
– P4 enp-2 with 4 elements (formula 121) **7**
6. Caudal ramus about 1.5 times as long as wide ..... ***P. kolarovi***
– Caudal ramus at least twice as long as wide ..... ***P. livingstoni***
7. P1 exopod 2-segmented **8**
– P1 exopod 3-segmented **12**
8. Caudal ramus conical and about 3 times as long as wide; P5 endopodal lobe ♀ with 3 setae ..... ***P. longipes***
– Caudal ramus cylindrical and not more than twice as long as wide; P5 endopodal lobe ♀ with 4 setae **9**
9. P5 exopod ♀ with 4 setae; P3 exp-3 ♂ with 7 setae/spines ..... ***P. karmensis***
– P5 exopod ♀ with 5 setae; P3 exp-3 ♂ with at most 6 setae/spines **10**
10. First and second abdominal somites with dorsal bilobate lappets; second antennulary segment ♀ without protuberance; P5 ♂ with 5 setae on exopod and 1 on endopodal lobe ..... ***P. lunata***
– First and second abdominal somites without dorsal bilobate lappets; second antennulary segment ♀ with small conical protuberance; P5 ♂ with different armature **11**
11. Caudal ramus 1.5 times as long as wide; P5 ♂ with 5 setae on exopod and none on endopodal lobe ..... ***P. spitzbergensis***
– Caudal ramus twice as long as wide; P5 ♂ with 4 setae on exopod and 1 on endopodal lobe ..... ***P. tenera***
12. Abdominal somites with a middorsal spinous process; P3 enp-2 ♀ with 4 elements; P3 endopod ♂ 2-segmented ..... ***P. quaterspinata***

– Abdominal somites without a middorsal spinous process; P3 enp-2 ♀ with 5–6 elements; P3 endopod ♂ 3-segmented with apophysis on enp-2 ..... **13**

13. Antennule ♀ 6-segmented; P3 enp-2 ♀ with 6 elements; P3 enp-2 ♂ apophysis shorter than endopod; longest seta of P5 exopod ♂ about 5 times the length of segment ..... ***P. zimmeri***

– Antennule ♀ 7-segmented; P3 enp-2 ♀ with 5 elements; P3 enp-2 ♂ apophysis as long or longer than endopod; longest seta of P5 exopod ♂ at most 2.5 times the length of segment **14**

14. Second antennulary segment ♀ without small conical protuberance; P5 exopod ♀ longer than wide, inner distal seta twice the length of proximal inner one; P5 exopod ♂ with 5 elements ..... ***P. pallaresae*, sp. n.**

– Second antennulary segment ♀ with small conical protuberance; P5 exopod ♀ semicircular, inner distal seta only slightly longer than proximal inner one; P5 exopod ♂ with 4 elements ..... ***P. obscura***

15. P2–P3 exp-3 with 2 outer spines; caudal ramus about 6 times as long as wide ..... ***P. lamellipes***

– P2–P3 exp-3 with 3 outer spines; caudal ramus distinctly shorter **16**

16. P4 exp-3 with 2 outer spines ..... ***P. panamensis***

– P4 exp-3 with 3 outer spines **17**

17. P4 exp-3 with 1 inner seta ..... ***P. taurina***

– P4 exp-3 with 2 inner setae **18**

18. P1 exopod 2-segmented **19**

– P1 exopod 3-segmented **22**

19. Second antennulary segment with distinct recurved hook-like process; P5 baseoendopod ♂ with 1 seta ..... ***P. pilosoma***

– Second antennulary segment with at most a small conical protuberance; P5 baseoendopod ♂ without setae **20**

20. Caudal ramus about 3.5 times as long as wide; P3 enp-2 ♀ with 2 inner setae; P3 endopod ♂ 2-segmented with 3 setae on enp-2 ..... ***P. macera***

– Caudal ramus at most 2.5 times as long as wide; P3 enp-2 ♀ with 3 inner setae; P3 endopod ♂ 2-segmented with 5 setae on enp-2 or 3-segmented with 4 setae on enp-3 ..... **21**

21. Caudal ramus about 2.5 times as long as wide; P3 enp-2 ♀ with 6 elements; P3 endopod ♂ 3-segmented ..... ***P. hyperborea***

– Caudal ramus about twice as long as wide; P3 enp-2 ♀ with 5 elements; P2 enp-1 ♂ as long as enp-2; P3 endopod ♂ 2-segmented ..... ***P. innae***

– Caudal ramus about 1.5 times as long as wide; P3 enp-2 ♀ with 6 elements; P2 enp-1 ♂ distinctly longer than enp-2; P3 endopod ♂ 2-segmented. ***P. perplexa***

22. Caudal ramus at least 3 times as long as wide **23**

– Caudal ramus at most 2.5 times as long as wide **26**

23. Cephalothorax with distinct integumental pits; P3 endopod ♀ with 5 elements ..... ***P. sculpta***

– Cephalothorax without distinct integumental pits; P3 endopod ♀ with 6 elements **24**

24. Antennule ♀ 7-segmented, without protuberance on second segment; caudal ramus at most 3 times as long as wide ..... ***P. octavia***

– Antennule ♀ 6-segmented, with protuberance on second segment; caudal ramus more than 3 times as long as wide; associated with *Maja squinado* **25**

25. P5 baseoendopod ♀ with 4 setae; caudal ramus 4 times as long as wide ..... ***P. royi***

– P5 baseoendopod ♀ with 5 setae; caudal ramus 3.5 times as long as wide .... ***P. majae***

26. Second antennulary segment with prominent recurved unguiform process ... ***P. dieuzeidei***

– Second antennulary segment with straight conical or spinous projection, or without any protuberance **27**

27. Caudal ramus at most 1.2 times as long as maximum width **28**

– Caudal ramus distinctly longer **29**

28. Antennule ♀ 6-segmented; P1 enp-1 1.7 times the length of exopod; P5 exopod ♀ with 5 elements ..... ***P. pacifica***

– Antennule ♀ 7-segmented; P1 enp-1 twice the length of exopod; P5 exopod ♀ with 4 elements ..... ***P. septemarticulata***

29. Second antennulary process with distinct straight spinous projection **30**

– Second antennulary process with or without small protuberance **31**

30. Antennule ♀ 7-segmented; P3 enp-2 ♀ with 6 elements; P5 exopod ♀ with 5 elements; innermost element of P5 exopod ♂setiform; caudal ramus 1.5 times as long as wide ..... ***P. meinerti***

– Antennule ♀ 7-segmented; P3 enp-2 ♀ with 6 elements; P5 exopod ♀ with 6 elements; innermost element of P5 exopod ♂ setiform; caudal ramus more than twice as long as wide ..... ***P. gurneyi***

– Antennule ♀ 6-segmented; P3 enp-2 ♀ with 5 elements; P5 exopod ♀ with 5 elements; innermost element of P5 exopod ♂ an enlarged plumose spine; caudal ramus 1.5 times as long as wide ..... ***P. problematica***

31. Antennule ♀ 7-segmented; P5 exopod ♂ with 4 elements; caudal ramus at least twice as long as wide **32**

– These characters not combined **33**

32. Caudal ramus 2.5 times as long as wide; P5 endopodal lobe ♀ with both inner setae equal in length P5; endopodal side P5 ♂ with conical projection ... ***P. congenera mediterranea***

– Caudal ramus twice as long as wide; P5 endopodal lobe ♀ with proximal inner seta distinctly longer than distal inner one; endopodal side P5 ♂ without conical projection ..... ***P. lacerdai***

33. Caudal ramus 2.5 times as long as wide; P5 exopod ♀ with 4 elements ..... ***P. ormieresi***
– Caudal ramus at most twice as long as wide; P5 exopod ♀ with 5 elements ..**34**
34. P3 enp-2 ♀ with 5 elements **35**
– P3 enp-2 ♀ with 6 elements **36**
35. Antennule ♀ 6-segmented; P1 enp-2 about 4.5 times as long as maximum width; P3 exopod ♂ strongly modified ..... ***P. echinata***
– Antennule ♀ 7-segmented; P1 enp-2 about 7 times as long as maximum width; P3 exopod ♂ not modified ..... ***P. gracilipes***
36. Antennule ♀ 6-segmented, with blunt protuberance on segment 2; P4 enp-2 about 1.5 times as long as maximum width; P3 exp-3 ♂ distal outer spine much shorter than middle outer one..... ***P. galapagoensis***
– Antennule ♀ typically 7-segmented and without protuberance on segment 2; P4 enp-2 about 2.8 times as long as maximum width; P3 exp-3 ♂ distal outer spine about as long as middle outer one..... ***P. congenera congenera***
– Antennule ♀ typically 6-segmented and with small pointed process on segment 2; P4 enp-2 about 3 times as long as maximum width; P3 exp-3 ♂ distal outer spine about twice as long as middle outer one ..... ***P. brevirostris***

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